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Establishment and new hosts of the non-native seed beetle *Stator limbatus* (Coleoptera, Chrysomelidae, Bruchinae) on acacias in Europe

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Abstract

Stator limbatus is a phytophagous beetle native to warm regions of North and Central America, feeding on Fabaceae seeds and one of the most polyphagous species within the subfamily Bruchinae, here reported for the first time in Europe and on new hosts. Adult beetles emerged from *Acacia* spp. seeds collected in the islands of Corsica (France), and Sardinia (Italy). The wide presence in Sardinia and Corsica supports the hypothesis that this alien species was introduced several years ago. In both islands, *S. limbatus* emerged from *Acacia mearnsii* seeds, with infestation rates of up to 74.2 and 90.8% in 2019 and 2020, respectively. This seed beetle also emerged from two previously unreported host species, *Acacia saligna* and *A. pycnantha*, showing highest infestation rates of 4.0 and 95.1%, respectively. Both *Acacia* species are reported as new host associations with *S. limbatus*. Overall, seed infestation rates recorded in 2019 and 2020 indicate that *S. limbatus* is well established and that Mediterranean bioclimatic conditions are suitable for its population increase in size. This study lays the foundations for further research on known and potential host species and the spread and distribution of *S. limbatus* in Europe.

Keywords
Acacia mearnsii, *Acacia pycnantha*, *Acacia saligna*, alien species, bean weevil, biological invasion, Mediterranean islands

Introduction

The global movement of people and goods and climate change are dramatically promoting the introduction of alien species in non-native environments in the Anthropocene (Kueffer 2017), resulting in a continuous accumulation of these species worldwide (Seebens et al. 2017; Venette and Hutchison 2021). This indicates that current measures to avoid new introductions of alien species are not always effective. Therefore, prevention, continuous monitoring in priority sites, early detection, and rapid intervention are of major importance for avoiding the establishment of new invasive alien species and agricultural or forestry pests and for reducing the spread of the existing ones, with special concern towards protected areas and natural ecosystems.

Among seed-feeding insects, the subfamily Bruchinae (Coleoptera, Chrysomelidae) beetles, renowned as bean weevils, is highly specific and likely the most important (van Klinken 2005). This family includes about 4,350 taxa distributed worldwide (Borowiec 1987). The beetle *Stator limbatus* (Horn, 1873) (Coleoptera, Chrysomelidae: Bruchinae) is an endophagous seed feeder of legumes (Fig. 1). Its native range spans from semiarid and xeric regions of southwestern United States and northern Mexico to dry tropical forests of Central America and northern South America. *Stator limbatus*

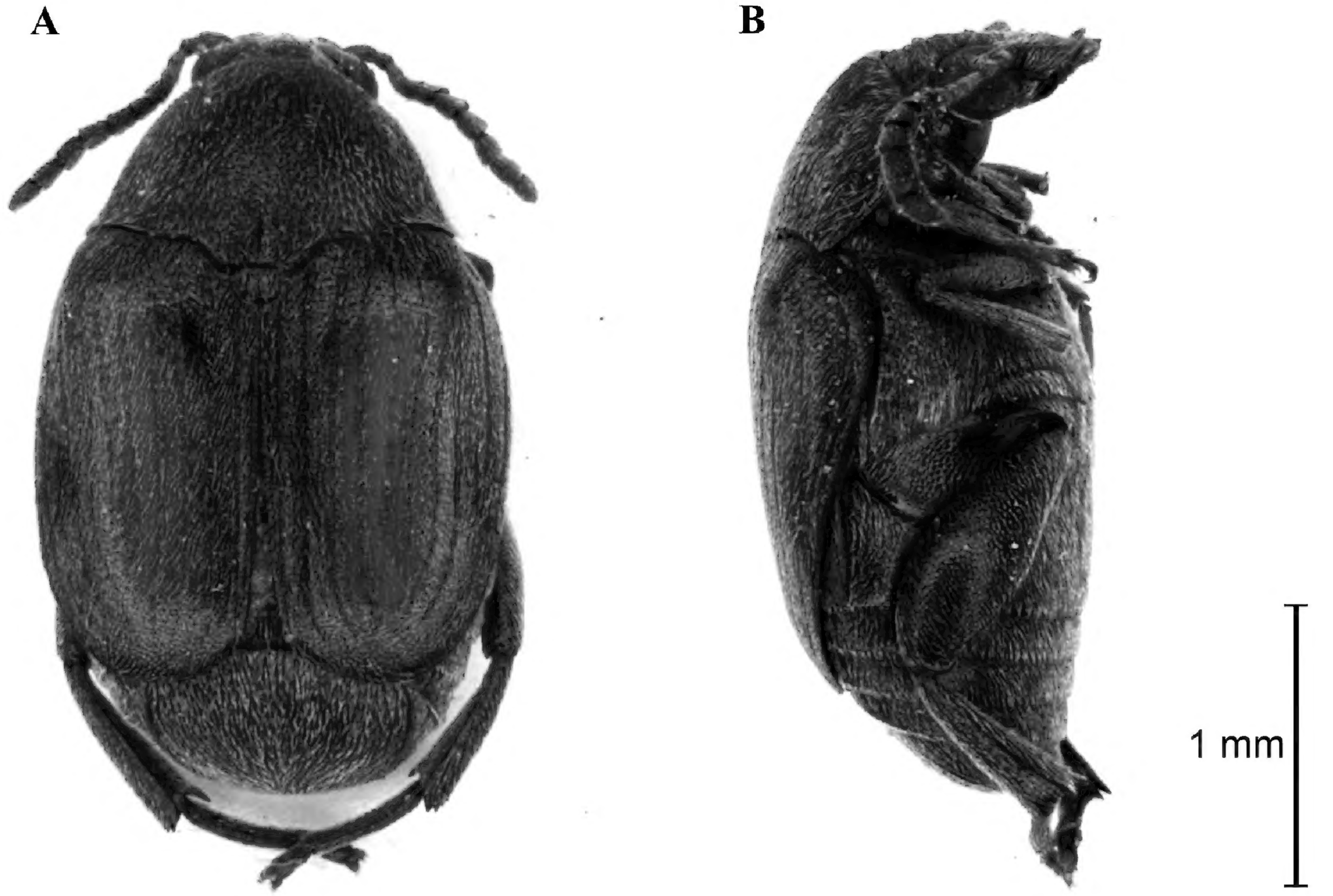

Figure 1. Habitus of adult *Stator limbatus* **A** dorsal and **B** lateral view.

has a generalist habit and a wide host range, as it has been collected from > 90 host plant species (de Jesús Parra-Gil et al. 2020), including many species of the genus *Acacia* s.l. In its native range, it affects mostly native species, but also about 20 non-native species (Stillwell et al. 2007). Despite that, host colonization of *S. limbatus* populations varies greatly among regions, and distinct populations exhibit host specialization at a local scale (Morse and Farrell 2005a, 2005b). Beetle populations are known to express phenotypic plasticity to host species by adapting pre-imaginal development time and body and egg size (Amarillo-Suarez and Fox 2006; Amarillo-Suarez et al. 2017).

Eggs are oviposited on mature seeds inside of dehiscent or partially dehiscent pods when they are still on the plant (Johnson 1981a; Kingsolver 2004). Females usually lay one egg per seed, and newly hatched larvae burrow into the seed integument beneath the egg, complete their development and pupate inside the same seed. In the case in which seeds are limiting, more eggs are deposited across a seed (Morse and Farrell 2005a). Beetles emerge from seeds as adults, mate and females start ovipositing within 24–48 hours, under laboratory conditions. Adults are facultatively aphagous, as they only require resources acquired during the pre-imaginal stage to complete development and reproduce (e.g. capital breeders) (Stillwell and Fox 2009). The generation time at 28 °C was determined to be 28–30 days (Amarillo-Suarez and Fox 2006).

Several species within the *S. limbatus* host range, such as *Acacia mearnsii* De Wild and *Acacia saligna* (Labill.) H.L.Wendl. native to Australia, have shown in Europe invasive potential and negative impacts on native species, to the extent that containment measures have been implemented (Lowe et al. 2000; European Union 2014; Tozzi et al. 2021). Therefore, monitoring the presence of seed beetles of invasive *Acacia* spp. in Europe is relevant in the perspective of finding and evaluating potential natural enemies able to slow the expansion and mitigate the adverse impacts of those species. Since *Acacia* in the broad sense have been grouped into distinct genera, e.g., *Mariosousa*, *Vachellia*, and *Senegalia*, and also other host species in the Leguminosae have been synonymized or renamed, a dedicated study would be required to define the current host range of the bruchid with valid plant names.

Outside its native range, *S. limbatus* has been reported in Hawaii (Bridwell 1920), South America (Oliveira and Costa 2009; Romero Gomez et al. 2009; Meiado et al. 2013), South Africa (Rink 2013), Iran (Boroumand 2010; Ghahari and Borowiec 2017), and United Arab Emirates (Delobel 2011), whereas reports from Mauritius, Saudi Arabia, Yemen, and Oman were unconfirmed (Rink 2013).

In the framework of an international project assessing the risk of invasion of selected alien species (**ALIEM**) (Inghilesi et al. 2018), some *Acacia* spp. seeds were tested in a germination test during which several individuals of *S. limbatus* adults emerged from seed lots of *A. mearnsii* seeds collected in Corsica (France) and Sardinia (Italy) in 2018. This insect species has not been yet recorded in Europe, so that new field collections were planned and carried out in 2019 and 2020.

The main aim of the present study was to investigate the establishment of *S. limbatus* in Sardinia and Corsica according to the traits described by Yus-Ramos et al. (2014) for alien seed beetles, as well as its host association and infestation levels. In addition, a literature search analysis was carried out to provide an updated inventory of host

species of *S. limbatus* with valid names, as understanding and predicting host shifts on other *Acacia* species is of pivotal importance in order to define its potential distribution in the Mediterranean Basin.

Materials and methods

Literature search analysis

Data sources used for investigating and updating the host range of *S. limbatus* were retrieved from major online databases, such as Google Scholar, Web of Science, Scopus, CAB abstracts, and ResearchGate. Papers were directly requested to authors and public repositories and libraries whenever inaccessible online. Different combinations of keywords were used in the literature search related to *S. limbatus* and its host range. Whenever possible, references were cross-checked and duplicates removed, giving priority to older records. Original plant names were collected from each reference, whereas country and locality records were reported whenever available.

Plant names were cross-checked taking into account relevant literature and different on-line databases, in particular Seigler et al. (2006), Kyalangalilwa et al. (2013), The Legume Phylogeny Working Group (LPWG 2017), World Flora Online (WFO) (2020), Plants of the World Online (POWO 2020), BHL (for original protologues), and the International Plant Name Index (IPNI) (2020). To our best knowledge, the accepted nomenclature was followed according to current taxonomic standards.

Seed collection

Legumes and loments (hereafter pods) with seeds of *A. mearnsii* were manually collected from adult trees naturalized in Corsica and Sardinia in September-November 2019. Seed sampling was carried out in Sardinia within two Special Areas of Conservation (SACs): "*Berchida e Bidderosa*" (Natura 2000 code ITB020012) (central eastern Sardinia) and "*Monte Linas – Marganai*" (Natura 2000 code ITB041111) (southwestern Sardinia), where the most important populations of *A. mearnsii* are located and the species shows clear invasive traits outcompeting with native vegetation. On the other hand, seeds in Corsica were collected along the eastern side of the island (Fig. 2). In Sardinia, seed sampling was extended to other *Acacia* species, i.e., *Acacia pycnantha* Benth. and *A. saligna*, not previously reported as host species but located nearby the sampling sites of *A. mearnsii*. Following the emergence of *S. limbatus* adults from all *Acacia* species sampled in 2019 (See Results), field collection of seeds was repeated in August-early September 2020 on the same species.

Acacia saligna is a widespread tree species in Corsica and Sardinia (Lozano et al. 2020), in particular along the coast, and severely impacts the characteristics of soils and diversity and structure of the Mediterranean shrublands (Celesti-Grapow et al. 2016; Tozzi et al. 2021). The other two *Acacia* species, although common, are much

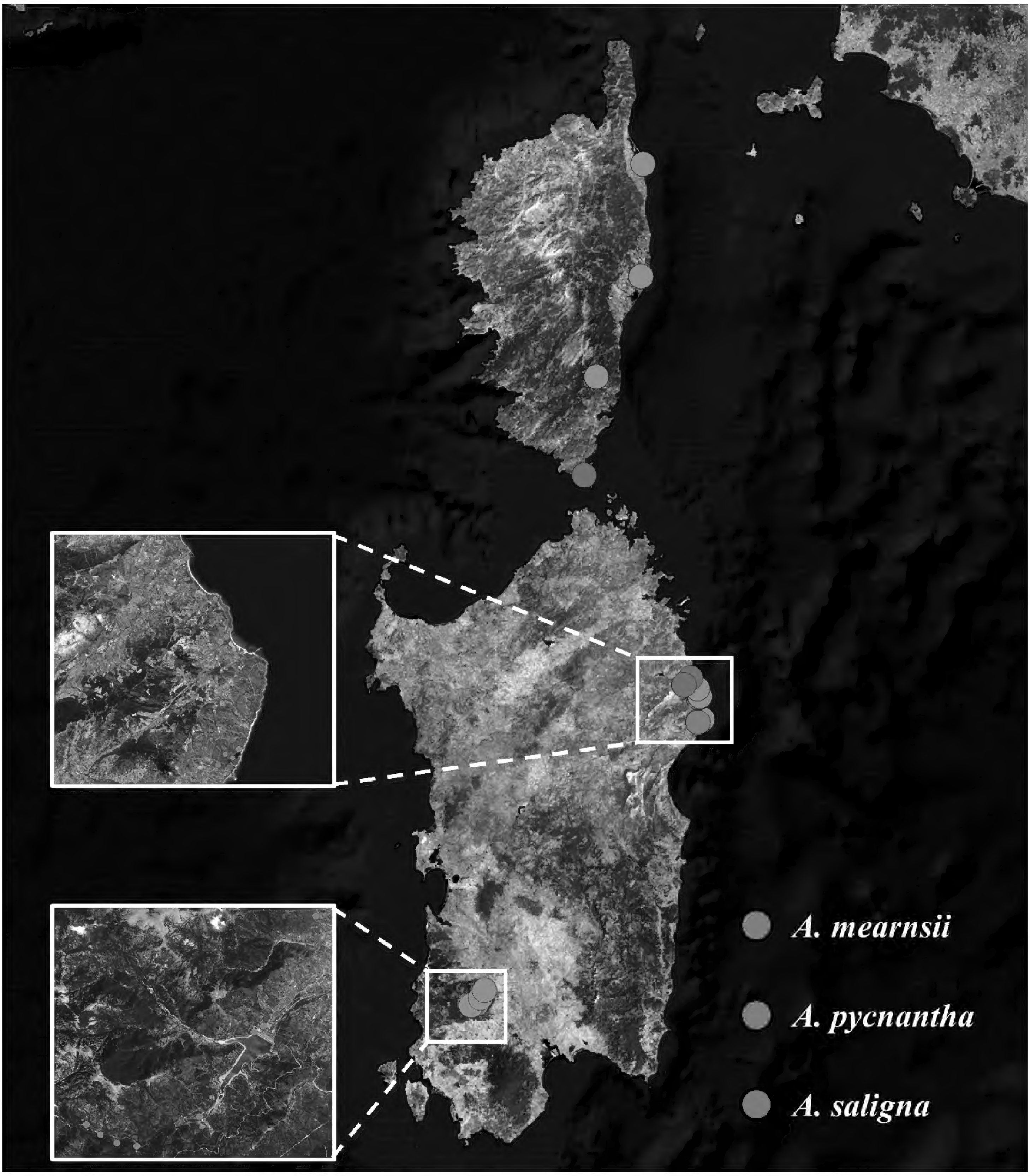

Figure 2. Map of sampling sites of *Acacia* spp. pods and seeds in Sardinia (Italy) and Corsica (France).

less widespread and form dense populations only in a limited number of sites. The width of the sampling site varied widely, ranging from a single tree to tree stands larger than 1,500 m^2, as well as the seed production of trees. Therefore, a minimum of 20 pods per tree, representative of seed production, were collected at random from 1–30 randomly-chosen trees. All in all, the sample size ranged from 75 to 8,500 seeds, depending on the width of the sampling site. In fact, seed production was generally very large in all the investigated *Acacia* spp. in both years and was not a limiting factor in seed sampling.

Seed examination

The collected pods and seeds were stored at laboratory temperature in cardboard envelopes sealed with adhesive tape, to avoid mold development and the escape of tiny seed beetles. Envelopes were opened after approximately three months and beetles were separated and identified morphologically using identification keys for *S. limbatus* adult detection (Johnson 1963; Kingsolver 2004). Seeds were further inspected under a dissecting microscope and the number of *Acacia* spp. seeds with emergence holes was determined in order to calculate the rate of infestation. Seeds of *A. saligna* showed very low seed infestation rates (see Results). However, in view of its importance as an invasive species and in order to point out a potential host shift, the presence of *S. limbatus* eggs on *A. saligna* seeds was also recorded.

Data analysis

The infestation rate, i.e., the percentage of seeds with *S. limbatus* emergence holes, as well as the percentage of *A. saligna* seeds with *S. limbatus* eggs were compared between sites or host species by Fisher exact test. The seed infestation rates were preliminary tested for data overdispersion by analyzing the χ^2 approximation of the residual variance (Venables and Ripley 2002; Zuur et al. 2009). Since overdispersion of data was found, overdispersion parameters were included in the corrected models using a quasi-binomial distribution followed by type II ANOVA to test for significance of main effects (Zuur et al. 2009). The seed infestation rate was the response variable, whereas "sampling area" and "year" were the fixed effects in 2019 and 2020, respectively. Corrected analyses were conducted using R software version 4.1.0 (R Development Core Team 2021) at the significance level of 0.05.

Results

Literature search analysis

The literature search on *S. limbatus* host plant species retrieved about 150 references. After a careful nomenclatural revision, the host range of *S. limbatus*, as so far described in literature, includes 37 plant genera belonging to three of the six subfamilies in the family Fabaceae:

subfamily Caesalpinioideae: *Acacia* (16 species), *Acaciella* (2), *Albizia* (10), *Caesalpinia* (1), *Calliandra* (4), *Cassia* (4), *Cercidium* (4), *Chloroleucon* (2), *Delonix* (1), *Desmanthus* (1), *Ebenopsis* (2), *Enterolobium* (2), *Havardia* (4), *Hesperalbizia* (1), *Leucaena* (3), *Lysiloma* (4), *Mariosousa* (4), *Mimosa* (1), *Neptunia* (1), *Painteria* (1), *Parkinsonia* (3), *Piptadenia* (2), *Pithecellobium* (5), *Prosopis* (5), *Pseudopiptadenia* (1), *Pseudosamanea* (1), *Senegalia* (15), *Sphinga* (1), *Vachellia* (2), *Wallaceodendron* (1), and *Zapoteca* (1);

subfamily Cercidoideae: *Bauhinia* (1);
subfamily Papilionoideae: *Arachis* (1), *Butea* (1), *Erythrina* (1), *Glycine* (1), and *Sesbania* (1).

Most host species belong to the subfamily Caesalpinioideae (105), 96 of which to the clade mimosoid, followed by Papilionoideae (5) and a single species of Cercidoideae. The list also comprises the following eight species included as non-host, experimental hosts and uncertain reports: *Calliandra humilis* Benth., *Cercidium texanum* A.Gray, *Delonix regia* (Bojer ex Hook.) Raf., *Prosopis juliflora* (Sw.) DC., *Prosopis velutina* Wooton, *Senegalia ataxacantha* (DC.) Kyal. & Boatwr (syn. *A. ataxacantha* DC.), *Vachellia constricta* (Benth.) Seigler & Ebinger, and *Vachellia farnesiana* (L.) Wight & Arn. (Bridwell 1920; Johnson 1981b; Fox et al. 1996, 2006; Kingsolver 2004; Rink 2013). The comprehensive host range of *S. limbatus* is provided with up-to-date nomenclature of host species on Table 1.

Seed infestation

The field surveys carried out in 2019–2020 demonstrated the presence of the seed-feeding beetle *S. limbatus* both in Sardinia (Italy) and Corsica (France) islands on the host plant *A. mearnsii* (Table 1). In Sardinia, the beetle emerged from seeds collected in all the 14 sites in both the central eastern and southwestern sampling areas. In 2019, the infestation rates ranged from 24.3 to 74.2% and from 39.3 to 83.4% in *Berchida-Bidderosa* and *Monte Linas – Marganai* areas, respectively, showing significant differences among sampling sites (Fisher tests: $\chi^2 = 1074.85$; $df = 5$; $P < 0.001$ and $\chi^2 = 404.83$; $df = 7$; $P < 0.001$, respectively) (Table 1). Overall, the seed infestation rate by *S. limbatus* did not differ between central eastern and southwestern sampling areas ($F = 0.496$; $df = 1.13$; $P = 0.494$). In 2020, the infestation in the central eastern sampling sites also differed significantly among sites (range = 85.4–90.8%) (Fisher test: $\chi^2 = 31.42$; $df = 5$; $P < 0.001$), and increased significantly compared to 2019 ($F = 16.206$; $df = 1.11$; $P = 0.002$). A large majority of *A. mearnsii* seeds (≥ 96.5% of seeds sampled in the various sites) showed *S. limbatus* eggs (up to 18 eggs in a single seed) and ≥ 98.4% of the infested seeds exhibited a single exit hole (Fig. 3A).

Acacia pycnantha trees sampled in central eastern Sardinia in both 2019 and 2020 (site 1) showed the highest infestation levels (85.1 and 95.1%, respectively) compared to *A. mearnsii* sites in the same area (Table 1). Of *A. pycnantha* infested seeds sampled in 2019 and 2020, 29.5 and 45.2%, respectively, exhibited two exit holes and up to 28 eggs were recorded in a single seed (Fig. 3B). Both the percentage of infested seeds and seeds with two holes increased significantly from 2019 to 2020 (Fisher tests: $\chi^2 = 48.73$; $df = 1$; $P < 0.001$ and $\chi^2 = 24.03$; $df = 1$; $P < 0.001$, respectively).

Pods and seeds of *A. saligna* were collected in the surroundings of infested *A. mearnsii* and *A. pycnantha* trees in two and nine sites in central eastern Sardinia (Table 2). The infestation rate was very low in both years and was significantly the highest at the site 5 in both 2019 (4%) (Fisher test: $\chi^2 = 6.32$; $df = 1$; $P = 0.033$) and 2020 (2.6%) (Fisher test: $\chi^2 = 53.74$; $df = 8$; $P < 0.001$). However, *S. limbatus* eggs were recorded on

Table 1. Updated global host range of *Stator limbatus* following a literature search analysis and review of valid plant names.

Host species			Country (Locality)
Host plant valid name †	Original name in the Reference	References	
Subfamily Caesalpinioideae			
Acacia baileyana F.Muell.	*Acacia baileyana* F. Mueller	Johnson and Kingsolver 1976	USA (California)
Acacia confusa Merr.	*Acacia confusa*	Swezey 1928; Zacher 1952	USA (Hawaii)
Acacia cultriformis A.Cunn. ex G.Don	*Acacia cultriformis* A.Cunn. ex G.Don	Johnson and Kingsolver 1976	
Acacia cyclops A.Cunn. ex G.Don	*Acacia cyclops*	Rink 2013	South Africa (Yzerfontein)
Acacia goldmanii (Britton & Rose) Wiggins	*Acacia goldmanii* (Br. & Rose) Wiggins	Johnson 1979	Mexico
Acacia koa A.Gray	*Acacia koa*	Swezey 1924	USA (Hawaii)
	Acacia koa Gray	Stein 1983	USA (Hawaii)
Acacia leptoclada Benth.	*Acacia leptoclada*	Romero Gomez et al. 2009	
Acacia mangium Willd.	*Acacia mangium* Willd.	Pereira et al. 2004; Medina and Pinzón-Florián 2011; Mojena et al. 2018	Brazil (Mato Grosso, Roraima), Colombia
Acacia mearnsii De Wild.	*Acacia mearnsii* De Wild.	Oliveira and Costa 2009; Cocco et al. (present paper)	Brazil (Rio Grande do Sul), France, Italy
	Acacia mearnsii	Fox et al. 2006; Rink 2013	South Africa (Tokai, Western Cape)
Acacia melanoxylon R.Br.	*Acacia melanoxylon* R.Br.	Johnson and Kingsolver 1976	
Acacia pycnantha Benth.	*Acacia pycnantha* Benth.	Cocco et al. (present paper)	Italy
Acacia podalyriifolia A.Cunn. ex G.Don	*Acacia podalyriifolia* A. Cunningham ex G.Don.	Garlet et al. 2011	Brazil (Rio Grande do Sul)
Acacia retinodes Schltdl.	*Acacia retinodes* Schlect.	Johnson and Kingsolver 1976	USA (California)
Acacia retusa (Jacq.) R.A.Howard	*Acacia retusa* (Jacq.) R.A.Howard	Johnson and Kingsolver 1976	Costa Rica
Acacia richii A.Gray	*Acacia richei* (sic) (*richii*)	Kingsolver 2004	
Acacia saligna (Labill.) H.L.Wendl.	*Acacia saligna* (Labill.) H.L.Wendl.	Cocco et al. (present paper)	Italy, France
Acacia sp.	*Acacia* sp.	Johnson 1984; Boroumand 2010; Ghahari and Borowiec 2017	Guatemala, Iran (Bushehr), Mexico
Acaciella angustissima (Mill.) Britton & Rose	*Acacia angustissima* (Mill.) Kuntze	Johnson and Kingsolver 1976; Johnson 1984, 1995	Colombia, Mexico, USA (Arizona, Texas), Venezuela
	Acacia angustissima	Morse and Farrell 2005a	Mexico, USA (Texas)
	Acacia angustissima angustissima	Kingsolver 2004	
Acaciella goldmanii Britton & Rose	*Acacia macmurphyi* Wiggins	Hetz and Johnson 1988	Mexico
Albizia adinocephala (Donn.Sm.) Britton & Rose ex Record	*Albizzia* (sic) (*Albizia*) *adinocephala*	Janzen 1980	Costa Rica
Albizia berteriana (DC.) Fawc. & Rendle	*Pithecellobium fragrans*	Romero Gomez et al. 2009	
Albizia berteroana (Balb. ex DC.) M.Gómez	*Albizia berteroana*	Romero Gomez et al. 2009	
Albizia caribaea (Urb.) Britton & Rose	*Albizia caribaea* (Urban) Britton & Rose	Johnson 1984	Honduras
	Albizzia (sic) (*Albizia*) *caribaea*	Janzen 1980	Costa Rica
	Albizia caribaea	Romero Gomez et al. 2009	
	Albizia niopoides var. *niopoides*	Romero Gomez et al. 2009	
Albizia chinensis (Osbeck) Merr.	*Albizzia* (sic) (*Albizia*) *chinensis*	Zacher 1952	
Albizia julibrissin Durazz.	*Albizia julibrissin*	Fox et al. 2006	
Albizia lebbeck (L.) Benth.	*Albizia lebbeck* Benth.	Lugo-García et al. 2015	Mexico
	Albizia lebbek (sic) *lebbeck* (L.) Benth.	Hetz and Johnson 1988; Johnson 1995	Mexico, Venezuela
	Albizzia lebbek (sic) (*Albizia lebbeck*)	Bridwell 1920	USA (Hawaii)
	Albizzia (sic) (*Albizia*) *lebbeck* (L.) Benth.	Nascimento 2009	Brazil (Rio de Janeiro)

Host species			Country (Locality)
Host plant valid name †	**Original name in the Reference**	**References**	
Albizia saman (Jacq.) Merr.	*Samanea saman*	Bridwell 1920; Morse and Farrell 2005a	Panama, USA (Hawaii), Venezuela
	Pithecolobium (sic) (*Pithecellobium*) (= *Samanea*) *saman*	Zacher 1952	
	Pithecellobium saman (Jacq.) Merrill	Johnson 1984	Guatemala
	Pithecellobium saman (Jacquin) Bentham	Johnson 1995	Ecuador, Venezuela
	Pithecellobium saman	Janzen 1980	Costa Rica
	Samanea saman (Jacq.) Merrill	Johnson and Kingsolver 1976	Costa Rica
Albizia saponaria Blume ex Miq.	*Albizia saponaria*	Kingsolver 2004	
Albizia sinaloensis Britton & Rose	*Albizia sinaloensis* Britt. & Rose	Hetz and Johnson 1988; Johnson 1995	Mexico
Albizia sp.	*Albizia* sp.	Johnson 1984, 1995	Brazil (Rio de Janeiro), Ecuador, Honduras, Venezuela
Caesalpinia pulcherrima (L.) Sw.	*Caesalpinia pulcherrima*	Fox et al. 2006	
Calliandra calothyrsus Meisn.	*Calliandra calothyrsus* Meissn.	Johnson and Lewis 1993	Nicaragua
Calliandra eriophylla Benth.	*Calliandra eriophylla* Bentham	Johnson 1979	USA (Arizona)
Calliandra houstoniana (Mill.) Standl.		Johnson 1984	Mexico, Guatemala
Calliandra houstoniana var. *calothyrsus* (Meissn.) Barneby	*Calliandra confusa* Sprague & Riley	Johnson 1984	Panama
Calliandra humilis Benth. ‡	*Calliandra humilis* ‡	Johnson 1981b	
	Calliandra humilis humilis	Kingsolver 2004	
Calliandra humilis var. *reticulata* (A.Gray) L.D.Benson	*Calliandra humilis reticulata*	Kingsolver 2004	
Calliandra sp.	*Calliandra* sp.	Johnson and Kingsolver 1976; Johnson 1984; Morse and Farrell 2005a	Costa Rica, Mexico, Venezuela
Cassia fistula L.	*Cassia fistula*	Kingsolver 2004	
Cassia grandis L.f.	*Cassia grandis*	Kingsolver 2004	
Cassia javanica L.	*Cassia javanica javanica*	Kingsolver 2004	
Cassia javanica subsp. *nodosa* (Buch.-Ham. ex Roxb.) K.Larsen & S.S.Larsen	*Cassia javanica indochinensis*	Kingsolver 2004	
Cassia moschata Kunth * *Cassia leiandra* Benth. *	*Cassia moschata*	Morse and Farrell 2005b	
Cercidium floridum Torr.	*Cercidium floridum* subsp. *floridum*	Romero Gomez et al. 2009	
	Parkinsonia florida	Kingsolver 2004; Fox et al. 2006	
	Cercidium torreyanum	Zacher 1952	
	Cercidium floridum Bentham	Johnson and Kingsolver 1976	USA (Arizona, California)
	Cercidium floridum (Benth.)	Fox et al. 1996, 2001; Stillwell and Fox 2005	USA (California)
Cercidium macrum I.M.Johnst.	*Parkinsonia texana* var. *macra*	Romero Gomez et al. 2009	
	Parkinsonia texana macra	Kingsolver 2004	
	Parkinsonia macra (Johnst.)	Fox et al. 1996	
	Parkinsonia macra	Nilsson and Johnson 1993	Mexico, USA (Texas)
Cercidium microphyllum Rose & I.M.Johnst.	*Cercidium microphyllum* (Torr.) Rose & Johnst.	Johnson and Kingsolver 1976	Mexico, USA (Arizona)
	Cercidium microphyllum (Benth.)	Fox et al. 2001	USA (California)
	Cercidium microphyllum	Morse and Farrell 2005a	USA (Arizona)
	Parkinsonia microphylla	Stilwell and Fox 2005	
Cercidium texanum A.Gray ‡	*Parkinsonia texana texana*	Kingsolver 2004	
	Parkinsonia texana (A.Gray) S.Watson ‡	Fox et al. 1996	USA (Texas)
Cercidium sp.	*Cercidium* sp.	Johnson 1984	Mexico

Host species			Country (Locality)
Host plant valid name †	**Original name in the Reference**	**References**	
Chloroleucon mangense (Jacq.) Britton & Rose	*Chloroleucon mangense*	Morse and Farrell 2005b	
	Chloroleucon mangense (Jacquin) Macbride	Johnson 1995	Venezuela
Chloroleucon tenuiflorum (Benth.) Barneby & J.W.Grimes	*Pithecellobium scalare* Griseb.	Johnson 1984	Brazil (Rio de Janeiro)
Delonix regia (Bojer ex Hook.) Raf. §	*Delonix regia* §	Kingsolver 2004	
Desmanthus bicornutus S.Watson	*Desmanthus bicornutus*	Kingsolver 2004	
Ebenopsis confinis (Standl.) Britton & Rose	*Ebenopsis confinis*	Romero Gomez et al. 2009	
Ebenopsis ebano (Berland.) Barneby & J.W.Grimes	*Ebenopsis ebano*	Romero Gomez et al. 2009	
	Chloroleucon ebano	Nilsson and Johnson 1993	USA (Arizona)
	Pithecellobium ebano	Kingsolver 2004	
	Siderocarpus flexicaule (sic) (*Siderocarpos flexicaulis*)	Cushman 1911	USA (Texas)
Ebenopsis sp.	*Siderocarpus* (sic) (*Siderocarpos*) sp.	Zacher 1952; Romero Gomez et al. 2009	
Enterolobium contortisiliquum (Vell.) Morong	*Enterolobium contortisiliquum* (Vell.) Morong	Meiado et al. 2013	Brazil (Pernambuco)
Enterolobium timbouva Mart.	*Enterolobium timbouva* Mart.	Meiado et al. 2013	Brazil (Pernambuco)
Havardia acatlensis (Benth.) Britton & Rose	*Havardia acatlensis*	Romero Gomez et al. 2009	
Havardia mexicana (Rose) Britton & Rose	*Havardia mexicana*	Romero Gomez et al. 2009	
	Pithecolobium (sic) (*Pithecellobium*) *mexicanum* F. N. Rose	Johnson and Kingsolver 1976	
Havardia pallens (Benth.) Britton & Rose	*Pithecellobium pallens* (Bentham) Standl.	Johnson and Kingsolver 1976	USA (Texas)
	Havardia pallens	Morse and Farrell 2005a	Mexico
	Pithecolobium (sic) (*Pithecellobium*) *brevifolium* Bentham	Johnson and Kingsolver 1976	
Havardia sonorae (S.Watson) Britton & Rose	*Havardia sonorae*	Romero Gomez et al. 2009	
	Pithecellobium sonorae S. Wats.	Johnson and Kingsolver 1976	Mexico
Hesperalbizia occidentalis (Brandegee) Barneby & J.W.Grime	*Albizia plurijuga*	Romero Gomez et al. 2009	Mexico
	Albizia occidentalis Brandegee	Hetz and Johnson 1988	
Leucaena diversifolia (Schltdl.) Benth.	*Leucaena diversifolia*	Romero Gomez et al. 2009	
	Acacia diversifolia	Romero Gomez et al. 2009	
Leucaena leucocephala (Lam.) de Wit	*Leucaena leucocephala* (Lam.) de Wit.	Johnson 1984	Mexico
Leucaena leucocephala subsp. *glabrata* (Rose) Zárate	*Leucaena leucocephala* subsp. *glabrata*	Romero Gomez et al. 2009	
Leucaena pulverulenta (Schltdl.) Benth.	*Leucaena pulverulenta* (Schl.) Bentham	Johnson and Kingsolver 1976	USA (Texas)
Leucaena trichandra (Zucc.) Urb.	*Leucaena diversifolia* subsp. *stenocarpa*	Romero Gomez et al. 2009	
	Leucaena guatemalensis Britt. & Rose	Johnson 1979	Mexico
	Leucaena guatemalensis (Britt. & Rose)	Hetz and Johnson 1988	Mexico
Lysiloma acapulcense (Kunth) Benth.	*Lysiloma acapulcense*	Romero Gomez et al. 2009	Mexico
	Lysiloma acapulcensis (sic) (*acapulcense*) Bentham	Hetz and Johnson 1988	Honduras
	Lysiloma acapulcensis (sic) (*acapulcense*) Kunth. Benth.	Johnson 1984	Guatemala
Lysiloma divaricatum (Jacq.) J.F.Macbr.	*Lysiloma divaricata* (Jacq.) MacBride	Johnson and Kingsolver 1976; Johnson 1984	Mexico
	Lysiloma divaricada (sic) (*divaricata*)	de Lorea Barocio 2006	
	Lysiloma divaricatum	Romero Gomez et al. 2009	
	Lysiloma microphyllum	Romero Gomez et al. 2009	

Host species			Country (Locality)
Host plant valid name †	**Original name in the Reference**	**References**	
Lysiloma latisiliquum (L.) Benth.	*Lysiloma latisiliquum* (L.) Benth.	Johnson 1984	Mexico
Lysiloma tergeminum Benth.	*Lysiloma tergeminum*	Romero Gomez et al. 2009	
Lysiloma watsonii Rose	*Lysiloma watsonii*	Romero Gomez et al. 2009	
	Lysiloma thornberi Britt. & Rose	Johnson 1979	USA (Arizona)
	Lysiloma thornberi	Zacher 1952	
	Lysiloma microphylla thornberi	Kingsolver 2004	
	Lysiloma microphyllum var. *thornberi*	Romero Gomez et al. 2009	
Lysiloma sp.	*Lysiloma* sp.	Johnson and Kingsolver 1976; Johnson 1984	Costa Rica; Mexico
Mariosousa acatlensis (Benth.) Seigler & Ebinger	*Acacia acatlensis* Bentham	Johnson and Kingsolver 1976	Mexico
Mariosousa coulteri (Benth.) Seigler & Ebinger	*Acacia coulteri* Bentham	Johnson and Kingsolver 1976	Mexico
	Acacia coulteri	Romero Gomez et al. 2009	
	Mariosousa coulteri	Lugo-Garcia et al. 2015	
	Acacia near *coulteri* Bentham	Johnson and Kingsolver 1976	Mexico
Mariosousa heterophylla (Benth.) Seigler & Ebinger	*Acacia willardiana* Rose	Johnson and Kingsolver 1976	Mexico
Mariosousa millefolia (S.Watson) Seigler & Ebinger	*Acacia millefolia* Wats.	Johnson and Kingsolver 1976	USA (Arizona)
Mimosa distachya var. *laxiflora* (Benth.) Barneby	*Mimosa laxiflora* Benth.	Lugo-García et al. 2015	Mexico
Mimosa sp.	*Mimosa* sp.	de Lorea Barocio 2006; Romero Gomez et al. 2009	Mexico
Neptunia plena (L.) Benth.	*Neptunia plena*	Kingsolver 2004	
Painteria leptophylla (DC.) Britton & Rose	*Painteria leptophylla* (DC.) Britton & Rose	de Jesús Parra-Gil et al. 2020	Mexico
Parkinsonia aculeata L.	*Parkinsonia aculeata* Linnaeus	Johnson and Kingsolver 1976	Mexico, USA (Arizona, Texas)
	Parkinsonia aculeata	Morse and Farrell 2005a	USA (Texas)
	Acacia aculeata	Zacher 1952	
Parkinsonia florida subsp. *peninsulare* (Rose) J.E.Hawkins & Felger	*Cercidium floridum* subsp. *peninsulare*	Romero Gomez et al. 2009	
Parkinsonia praecox (Ruiz & Pav.) Hawkins	*Parkinsonia praecox*	Romero Gomez et al. 2009	
	Cercidium praecox (Ruiz & Pav.) Harms	Johnson and Kingsolver 1976	Mexico
Piptadenia flava (Spreng. ex DC.) Benth.	*Piptadenia flava*	Janzen 1980	Costa Rica
	Parkinsonia flava	Romero Gomez et al. 2009	
Piptadenia obliqua (Pers.) J.F.Macbr.	*Piptadenia obliqua* (Persoon) Macbride	Johnson 1995	Venezuela
	Piptadenia oblique	Morse and Farrell 2005a	Venezuela
Pithecellobium candidum (Kunth) Benth.	*Pithecellobium candidum* Bentham	Johnson 1995	Ecuador
Pithecellobium dulce (Roxb.) Benth.	*Pithecellobium dulce* (Roxb.) Bentham	Johnson and Kingsolver 1976; Johnson 1984, 1995	Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, Mexico, Venezuela
	Pithecellobium dulce	Morse and Farrell 2005a; de Lorea Barocio 2006	Mexico, Ecuador, Venezuela
	Pithecolobium (sic) (*Pithecellobium*) *dulce*	Bridwell 1920; Zacher 1952	USA (Hawaii)
Pithecellobium excelsum (Kunth) Mart.	*Pithecellobium excelsum* Bentham	Johnson 1995	Ecuador
	Pithecellobium excelsum	Morse and Farrell 2005a	Ecuador
Pithecellobium oblongum Benth.	*Pithecellobium oblongum*	Janzen 1980	Costa Rica
Pithecellobium unguis-cati (L.) Benth.	*Pithecellobium unguis-cati*	Morse and Farrell 2005a	Venezuela
	Pithecolobium unguiscatae (sic) (*Pithecellobium unguis-cati*)	Bridwell 1920	USA (California)

Host species			Country (Locality)
Host plant valid name †	**Original name in the Reference**	**References**	
Pithecellobium sp.	*Pithecellobium* sp.	Johnson and Kingsolver 1976	El Salvador
	Pithecolobium (sic) (*Pithecellobium*) sp.	Bridwell 1920	USA (Hawaii)
Prosopis chilensis (Molina) Stuntz	*Prosopis chilensis*	Romero Gomez et al. 2009	
	Prosopis chilensis (= *juliflora*)	Zacher 1952	
Prosopis farcta (Banks & Sol.) J.F.Macbr.	*Prosopis farcta*	Boroumand 2010	Iran (Bushehr and Yazd)
	Prosopis farcta (Banks & Soland.) Macbr.	Shamszadeh et al. 2017	Iran (Yazd)
Prosopis glandulosa var *glandulosa* Torr.	*Prosopis glandulosa glandulosa*	Kingsolver 2004	
Prosopis glandulosa var. *torreyana* (L.D.Benson) M.C.Johnst.	*Prosopis glandulosa torreyana*	Kingsolver 2004	
Prosopis juliflora (Sw.) DC. ‡	*Prosopis juliflora* ‡	Bridwell 1920; Kingsolver 2004; Fox et al. 2006	
Prosopis velutina Wooton ‡	*Prosopis velutina* ‡	Johnson 1981b	
Pseudopiptadenia inaequalis (Benth.) Rauschert	*Piptadenia inaequalis* Bentham	Johnson 1995	Venezuela
	Piptadenia inaequalis	Morse and Farrell 2005a	Venezuela
Pseudosamanea guachapele (Kunth) Harms	*Pseudosamanea guachapele*	Amarillo-Suárez et al. 2011	
	Albizia guachepele (sic) (*guachapele*) (HBK.) Dugand	Johnson 1995	Colombia
Senegalia ataxacantha (DC.) Kyal. & Boatwr ‡	*Acacia ataxacantha* ‡	Rink 2013	South Africa
Senegalia berlandieri (Benth.) Britton & Rose	*Acacia berlandieri* Bentham	Johnson and Kingsolver 1976	Mexico, USA (Texas)
	Acacia berlandieri	Amarillo-Suárez et al. 2011	USA (Texas)
Senegalia gaumeri (S.F.Blake) Britton & Rose	*Acacia gaumeri* Blake	Johnson 1984	Honduras, Mexico
	Acacia gaumeri	Morse and Farrell 2005a	Mexico
Senegalia gilliesii (Steud.) Seigler & Ebinger	*Acacia furcatispina*	Romero Gomez et al. 2009	
Senegalia glomerosa (Benth.) Britton & Rose	*Acacia glomerosa*	Romero Gomez et al. 2009	
	Acacia near *glomerosa* Bentham	Johnson and Kingsolver 1976	Mexico
Senegalia greggii (A.Gray) Britton & Rose	*Acacia greggii* A. Gray	Johnson and Kingsolver 1976	Mexico, USA (Arizona, California, Texas)
	Acacia greggii	Morse and Farrell 2005a; Amarillo-Suárez et al. 2011	USA (Arizona)
Senegalia hayesii (Benth.) Britton & Rose	*Acacia hayesii*	Romero Gomez et al. 2009	
Senegalia occidentalis (Rose) Britton & Rose	*Acacia occidentalis* Rose	Johnson and Kingsolver 1976	Mexico
Senegalia picachensis (Brandegee) Britton & Rose	*Acacia picachensis* T. S. Brandg.	Johnson 1984	Mexico
Senegalia polyphylla (DC.) Britton & Rose	*Acacia polyphylla* DC.	Johnson 1995; Johnson and Siemens 1995	Colombia, Venezuela
Senegalia riparia (Kunth) Britton & Rose	*Acacia riparia*	Romero Gomez et al. 2009	
Senegalia roemeriana (Scheele) Britton & Rose	*Acacia roemeriana* Scheele	Johnson and Kingsolver 1976	USA (Texas)
Senegalia tamarindifolia (L.) Britton & Rose	*Acacia tamarindifolia* (L.) Willdenow	Johnson 1995; Johnson and Siemens 1995	Venezuela
	Acacia tamarindifolia	Morse and Farrell 2005a	Martinique
Senegalia tenuifolia (L.) Britton & Rose	*Acacia tenuifolia* (L.) Willd.	Johnson and Kingsolver 1976; Johnson 1984	Costa Rica, Mexico
Senegalia wrightii (Benth.) Britton & Rose	*Acacia wrightii* Bentham	Johnson and Kingsolver 1976	USA (Texas)
	Acacia wrightii	Morse and Farrell 2005a	Mexico, USA (Texas)
Sphinga platyloba (DC.) Barneby & J.W.Grimes	*Sphinga platyloba*	Morse and Farrell 2005b	
	Pithecellobium platyloba (sic) (*platylobum*)	Janzen 1980	Costa Rica
	Havardia platyloba	Romero Gomez et al. 2009	
Vachellia constricta (Benth.) Seigler & Ebinger ‡	*Acacia constricta* ‡	Johnson 1981b	
Vachellia farnesiana (L.) Wight & Arn. ‡	*Acacia farnesiana* ‡	Bridwell 1920	
	Acacia farnesiana	Zacher 1952	

Host species			Country (Locality)
Host plant valid name †	Original name in the Reference	References	
Wallaceodendron celebicum Koord.	*Wallaceodendron celebicum*	Bryan 1932	USA (Hawaii)
Zapoteca portoricensis (Jacq.) H.M.Hern.	*Zapoteca portoricensis*	Morse and Farrell 2005b	
Subfamily Cercidoideae			
Bauhinia purpurea L.	*Bauhinia purpurea* L.	Fox et al. 2006	
Subfamily Papilionoideae			
Arachis hypogaea L.	*Arachis hypogaea*	Kingsolver 2004	
Butea monosperma (Lam.) Kunze	*Butea monosperma*	Romero Gomez et al. 2009	
	Erythrina monosperma	Zacher 1952	
Erythrina sandwicensis O.Deg.	*Erythrina sandwicensis*	Kingsolver 2004	
Glycine max (L.) Merr.	*Glycine max*	Kingsolver 2004	
Sesbania sp.	*Sesbania* sp.	Romero Gomez et al. 2009	

† Valid names following Kyalangalilwa et al. (2013), Plants of the World Online (POWO 2020), and World Flora Online (WFO) (2020). ‡ Non-host or experimental hosts. * Morse and Farrell (2005b) did not specify the authorship, it is therefore impossible to determine whether they referred to *Cassia moschata* Kunth or *Cassia leiandra* Benth, which are both accepted names. § Uncertain report (Kingsolver 2004).

up to 52.8 and 79.6% of *A. saligna* seeds in 2019 and 2020, respectively (Fig. 3C). A single seed harbored up to six eggs. The seed infestation rate ranged in 2020 from 0 to 2.6% regardless of the distance from infested *Acacia* spp. trees, whereas *A. saligna* seeds with the highest percentage of beetle eggs (sites 1, 4, 5, and 6, range 45.1–79.6%) were recorded on trees <5 m apart from infested trees (Table 2).

In Corsica, *S. limbatus* adults were recorded in all four sampling sites. In 2019, adults emerged in both eastern (site 19) and northeastern (site 18) sites from *A. mearnsii* seeds. Most seeds exhibited exit holes and egg chorions of *S. limbatus*, although a few individuals were recorded: four adults from site 19 and one from site 18. In 2020, *S. limbatus* adults were further recovered in sites 18 and 21, in which more than 400

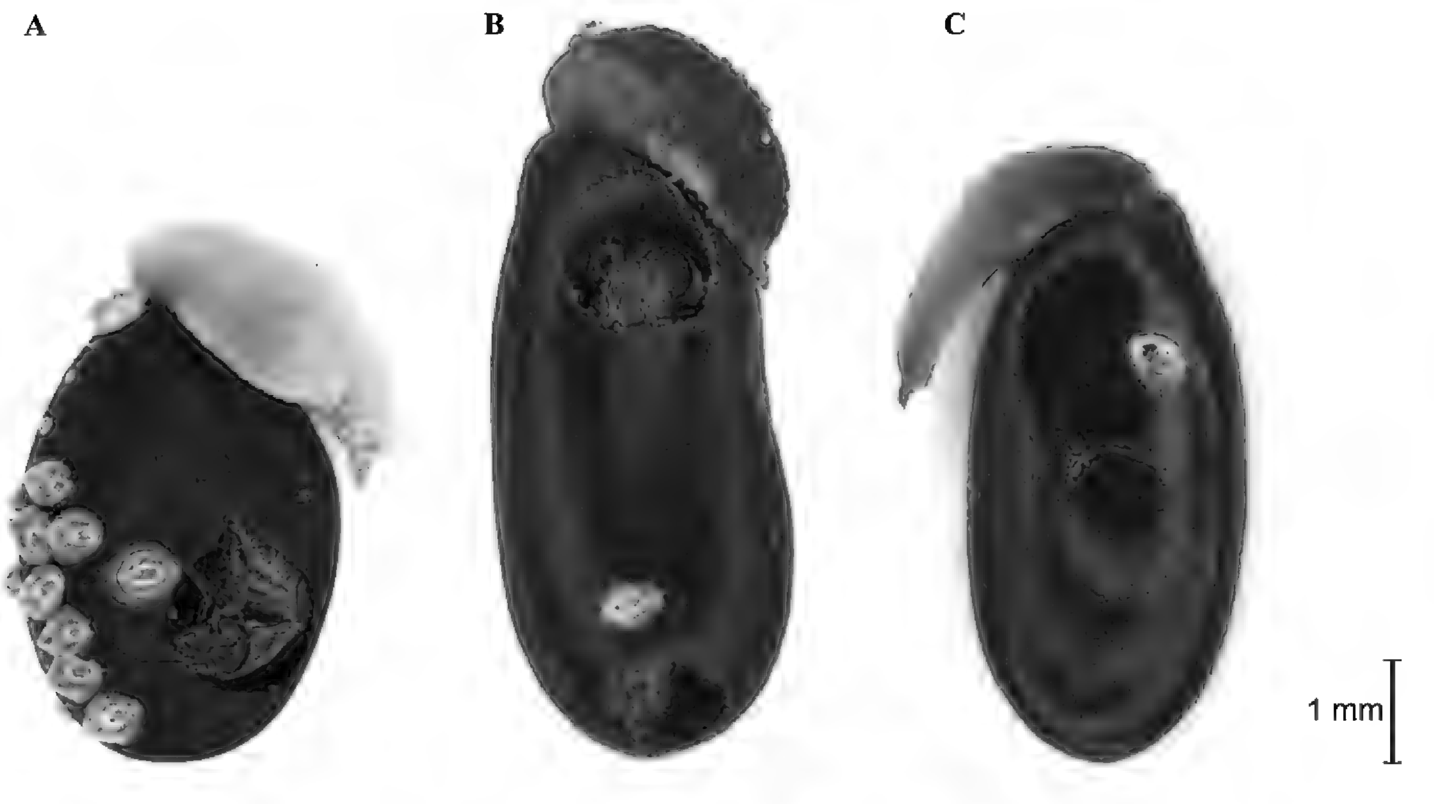

Figure 3. *Acacia* seeds (with arils on top) infested by *Stator limbatus*, with eggs and exit holes **A** *S. limbatus* adult emerging from an *Acacia mearnsii* seed with 11 eggs **B** *S. limbatus* adult emerging from *A. pycnantha* seed with two exit holes **C** *A. saligna* seed with a *S. limbatus* egg and one exit hole.

Table 2. Locations of sampling sites in Sardinia (Italy) and Corsica (France), and seed infestation rates of *Acacia pycnantha* and *A. mearnsii* by *Stator limbatus*.

Site no.	WGS84 Coordinates (°N, °E)	Sampling date	Host plant	Sampled seeds (no.)	Infestation rate (%) †
Sardinia, *Berchida-Bidderosa* area, 2019					
1	40.451995, 9.778190	18/09/2019	*A. pycnantha*	315	85.1 a
2	40.459980, 9.785646	18/09/2019	*A. mearnsii*	199	38.7 d
3	40.457190, 9.793082	18/09/2019, 01/10/2019	*A. mearnsii*	3459	74.2 b
4	40.463992, 9.798704	18/09/2019, 01/10/2019	*A. mearnsii*	1030	49.3 d
5	40.545390, 9.782090	18/09/2019	*A. mearnsii*	61	45.9 d
6	40.549220, 9.788000	18/09/2019, 01/10/2019	*A. mearnsii*	1137	24.3 e
7	40.578073, 9.777057	18/09/2019, 01/10/2019	*A. mearnsii*	3639	67.5 c
Sardinia, *Berchida-Bidderosa* area, 2020					
1	40.451995, 9.778190	10/08/2020	*A. pycnantha*	2415	95.1 a
2	40.459980, 9.785646	10/08/2020	*A. mearnsii*	1784	90.8 b
3	40.457190, 9.793082	10/08/2020	*A. mearnsii*	2234	89.0 bc
4	40.463992, 9.798704	10/08/2020	*A. mearnsii*	1704	86.5 d
5	40.545390, 9.782090	10/08/2020	*A. mearnsii*	1023	85.4 d
6	40.578073, 9.777057	10/08/2020	*A. mearnsii*	390	87.2 cd
7	40.549220, 9.788000	10/08/2020	*A. mearnsii*	1574	89.8 bc
Sardinia, *Monte Linas – Marganai* area, 2019					
10	39.421480, 8.716520	23/09/2019	*A. mearnsii*	226	61.9 cde
11	39.398540, 8.695790	23/09/2019	*A. mearnsii*	199	54.3 e
12	39.391094, 8.675427	23/09/2019	*A. mearnsii*	341	65.4 cd
13	39.396532, 8.658998	23/09/2019	*A. mearnsii*	671	66.6 c
14	39.393961, 8.663604	23/09/2019	*A. mearnsii*	980	59.8 de
15	39.391863, 8.669016	23/09/2019	*A. mearnsii*	951	79.4 b
16	39.420067, 8.713574	23/09/2019	*A. mearnsii*	1187	83.4 a
17	39.449340, 8.733530	23/09/2019	*A. mearnsii*	428	39.3 f
Corsica, 2019					
18	42.546699, 9.525582	29/10/2019	*A. mearnsii*	-	n.a.
19	42.125300, 9.510656	07/11/2019	*A. mearnsii*	-	n.a.
Corsica, 2020					
18	42.546576, 9.5246522	20/08/2020	*A. mearnsii*	-	n.a.
19	42.125065, 9.510606	20/08/2020	*A. mearnsii*	8500	56.0
21	41.380217, 9.222299	03/09/2020	*A. mearnsii*	-	n.a.

† Different letters within years indicate significant difference by Fisher exact test ($P < 0.05$). n.a. = not available.

Table 3. Locations of sampling sites in Sardinia (Italy) and Corsica (France), and seed infestation rates of *Acacia saligna* seeds by *Stator limbatus*.

Site no.	WGS84 Coordinates (°N, °E)	Sampling date	Distance from infested *Acacia* trees	Sampled seeds (no.)	Infestation rate (%) †	Seeds with *S. limbatus* eggs (%) †
Sardinia, *Berchida-Bidderosa* area, 2019						
4	40.463799, 9.799295	18/09/2019	< 5 m	156	0 b	44.9 a
5	40.545420, 9.782050	18/09/2019	< 5 m	75	4.0 a	52.8 a
Sardinia, *Berchida-Bidderosa* area, 2020						
1	40.451980, 9.778390	10/08/2020	< 5 m	1550	0 d	57.2 b
4	40.463799, 9.799295	10/08/2020	< 5 m	524	0.6 abc	60.7 b
5	40.545420, 9.782050	10/08/2020	< 5 m	116	2.6 a	79.6 a
	40.546396, 9.782224	10/08/2020	< 100 m	864	0.3 bcd	24.4 d
	40.546109, 9.781190	10/08/2020	< 100 m	867	0 d	18.0 e
6	40.549240, 9.788131	10/08/2020	< 5 m	859	0 d	45.1 c
	40.549022, 9.786670	10/08/2020	< 100 m	1237	0.2 bcd	22.5 d
8	40.618420, 9.743740	10/08/2020	> 100 m	981	0 d	3.0 g
9	40.592818, 9.710812	17/08/2020	> 100 m	596	0.2 bcd	8.9 f
Corsica, 2020						
20	41.380217, 9.222299	27/08/2020	-	4360	0.2	n.a.

† Different letters within years indicate significant difference by Fisher exact test ($P < 0.05$).

adults emerged from samples of *A. mearnsii* seeds of unknown sizes. In site 19, the infestation level by *S. limbatus* was 56.0%. Seeds of *A. saligna* were collected in site 20, where the infestation rate was 0.2%.

Discussion

The extensive collection of *S. limbatus* during the field surveys in 2019 and 2020 in Sardinia and Corsica following the first record in 2018 indicates that the seed beetle has found suitable climatic conditions and has established in Europe. *Stator limbatus* can be considered established according to the definition of Yus-Ramos et al. (2014), i.e., a species able to reproduce successfully in natural ecosystems. *Stator limbatus* exhibits biological features that could support its further spread in Europe. At first, this species has a wide host range worldwide, with about 15 species reported in Europe (Euro+Med 2021; GBIF 2021). Furthermore, its native geographic range includes diverse climates, spanning from dry forests of northern South America to deserts of Central America and southwestern United States (Stillwell and Fox 2009). In addition, this bruchid developed under laboratory conditions also on non-native species, including *Acacia cyclops* A.Cunn. G.Don and *S. ataxacantha* (syn. *A. ataxacantha*) (native to Australia and South Africa, respectively) (Rink 2013), as well as non-host species, such as *C. humilis*, *C. texanum*, *P. juliflora*, *P. velutina*, *V. constricta*, and *V. farnesiana* (Bridwell 1920; Johnson 1981b; Fox et al. 1996). Finally, *S. limbatus* have shown adaptive oviposition phenotypic plasticity in response to host species, as fewer and bigger eggs are laid on exotic or unfavorable hosts (Amarillo-Suarez et al. 2017). Such maternal egg-size plasticity is suggested to be an ancestral trait influencing the evolution of the diet breadth (Amarillo-Suárez and Fox 2006). Overall, the wide presence of host species of *S. limbatus* in Europe, its strong host shift potential, and climate adaptation suggest its possible spread in Mediterranean environments, and its presence in unsampled areas cannot be ruled out.

This species was recovered from *Acacia* spp. seeds in Sardinia, in multiple sites distant up to 150 km, and Corsica, in four areas distant about 130 km. Even though the country of first introduction in Europe remains undetermined, the wide presence of this alien insect in distant areas supports the hypothesis that its introduction occurred several years ago. The introduction of *S. limbatus* in Europe was most likely accidental and its detection unexpected. The pathway of first introduction is presently unknown, as no specific custom interception has so far been reported. With regard to pathways of secondary spread, in view of its wide host range and endophytic behavior of larvae, we may assume that it was introduced through movement of contaminated commodities, i.e., plants for planting, as a parasite of seeds (CBD 2014; Faulkner et al. 2020). In fact, after its first introduction, a secondary spread pathway may have occurred as a result of movement of contaminated plants (with pods) or seeds of *A. saligna*, *A. mearnsii*, and *A. pycnantha*, which are commonly planted in southern Europe and significantly traded. In addition, the very large number of different host species should be

taken into account (Table 1), as many are common ornamental, i.e., *Albizia* spp., *Leucaena* spp., *Parkinsonia* spp., and *Glycine max* (L.) Merr., or forestry and multipurpose species, i.e., *Acacia* spp., in the Mediterranean area. Therefore, in order to investigate the *S. limbatus* presence or intercept its introduction in areas nearby Sardinia and Corsica, specific monitoring plans on its host species should be set up in southern France and mainland Italy. Although the pathways of first introduction and secondary spread are generally not known for bruchid seed beetles, several authors suggest introductions through importation of seed or nursery stocks of host plant species for ornamental or forestry purposes, e.g., *Bruchidius terrenus* (Sharp, 1886) on *Albizia julibrissin* Durazz. and *Amblycerus robiniae* (Fabricius, 1781) on *Gleditsia triacanthos* L. in the United States (Kingsolver 2004; Hoebeke et al. 2009; Yus-Ramos et al. 2014).

The introduction of alien seed beetles in Europe shows an increasing trend in the last 20 years, in accordance with the worldwide trend described by Seebens et al. (2017). Beenen and Roques (2010) reported 14 Bruchinae alien species in Europe, seven of which introduced before 1900, three species in the period 1901–1950, two in 1951–2000, and finally two species reported from 2001 to 2010. Yus-Ramos et al. (2014) further extended the list of alien bruchids in Europe to a total of 42 species, including four recent introductions, namely *Bruchidius radiannae* Anton & Delobel, 2003 and *Caryedon acaciae* (Gyllenhal, 1833) on *Vachellia karroo* (Hayne) Banfi & Galasso (syn. *Acacia karroo* Hayne) in 2007 in Spain (Yus Ramos and Coello García 2007, 2008), *Acanthoscelides macrophthalmus* (Schaeffer, 1907) on *Leucaena leucocephala* (Lam.) de Wit in Cyprus in 2007 (Vassiliou and Papadoulis 2008), and *B. terrenus* on *A. julibrissin* in Bulgaria in 2009 (Stojanova 2010). Furthermore, *A. robiniae* was reported on *G. triacanthos* in Romania in 2018 following an unconfirmed report in Hungary in 1986 (Rădac et al. 2021). Therefore, according to literature reports, seven species of bruchids have been reported in Europe in the last 20 years. In both Corsica and Sardinia, *S. limbatus* larvae developed on seeds of *A. mearnsii*, a tree native to Australia which has shown to be invasive in Europe, South America, and Africa. This insect-host association has been previously reported in Brazil, where an infestation rate of 44.3% was observed (Oliveira and Costa 2009), and South Africa (Rink 2013). *Acacia mearnsii* is cultivated in Brazil for tannins, cellulose, and charcoal production (Garlet et al. 2011), whereas in Europe and in South Africa, presently, this species has a lower significant economic importance and is rather invasive (Souza-Alonso et al. 2017; Railoun et al. 2021).

In Sardinia, beetle adults emerged abundantly also from *A. pycnantha* seeds, and, interestingly, 45% of sampled seeds showed two exit holes, differently from *A. mearnsii* seeds which showed a single exit hole. This brings evidence that *A. pycnantha* seeds support the development of more than one larva of *S. limbatus*, most likely because of the bigger size of its seeds compared to those of *A. mearnsii*. In central eastern Sardinia, the infestation rate was more homogeneous among sampling sites in 2020 than in 2019, as the range decreased from 49.9% (24.3–74.2%) in 2019 to 5.4% (85.4–90.8%) in 2020. Moreover, infestation rates increased significantly on both *A. mearnsii* and *A. pycnantha*. However, the seed production of trees in the sampling sites was not quan-

titatively estimated being beyond the aims of the study. Estimates of seed infestation rates with no assessment of tree seed production and over such a short period, i.e. two years, prevent to infer on spatio-temporal population trends of *S. limbatus*. The same insect abundance can, in fact, cause high infestation rates in the event of low seed production or low rates when seed production is high. Nonetheless, although *Acacia* spp. seed production and accumulation may vary widely, Australian and African species usually produce large or very large quantities of seed and may have large soil-stored seed banks (Gibson et al. 2011). High production of seeds for the three investigated species has been observed both in the native and in the invaded ranges, e.g., *A. mearnsii* in South Africa (Impson et al. 2021), being one of the drivers of invasiveness at the global level. Indeed, large amounts of pods were observed on *Acacia* spp. trees as well as seeds in the topsoil in both 2019 and 2020 (A. Cocco, Y. Petit, pers. obs.). Furthermore, high numbers of seedlings were observed in the sampling sites with *A. mearnsii*.

Previous studies on infestation by *S. limbatus* on Fabaceae species reported seed damages of 15% on *E. timbouva* (Meiado et al. 2013), 19% on *Acacia mangium* Willd. (Mojena et al. 2018), and 70% on *Acacia podalyriifolia* A.Cunn. ex G.Don (Garlet et al. 2011) in Brazil. In Mexico, seed infestation rates of 16.8% were observed on *Painteria leptophylla* (DC.) Britton & Rose (de Jesús Parra-Gil et al. 2020) and 33.6% on *Mariosousa coulteri* (Benth.) Seigler & Ebinger by both *S. limbatus* and *Merobruchus santarosae* Kingsolver, 1989 (Coleoptera, Chrysomelidae) (Romero Gomez et al. 2009). Susceptibility to *S. limbatus* widely varied among hosts and areas; however, comparisons are difficult, as seed infestation rates are influenced by a number of abiotic and biotic factors, including seed availability and environmental conditions. Despite its recent report in South Africa, *S. limbatus* has not been reported infesting *A. pycnantha* seeds (Rink 2013; Magona et al. 2018).

A word of caution is in order with regard to *A. saligna* as a host species for *S. limbatus*. In fact, infestation rates were very low in both years and countries, and the highest values (4% in 2019 and 2.6% 2020) were observed in the same site. Nonetheless, infestation by *S. limbatus* on *A. saligna* seeds was not limited to a single site, as infested plants were observed in both Sardinia and Corsica. Moreover, beetle eggs were observed on up to 80% of *A. saligna* seeds, especially on plants near to infested *Acacia* spp. trees. This could be due to an opportunistic egg-laying behavior on the nearest alternative hosts. Furthermore, oviposition on *A. saligna* indicates that seeds had no antixenotic effect on female oviposition and oviposition is promoted by suitable hosts nearby. Chemical or physical barriers on *A. saligna* seeds preventing larval development cannot be ruled out and would require further investigations. Laboratory tests carried out in South Africa investigating the oviposition preference showed that *S. limbatus* females accepted *A. saligna* seeds for oviposition, together with seeds of *A. cyclops*, *A. mearnsii*, *Paraserianthes lophantha* (Willd.) I.C.Nielsen (invasive non-native species in South Africa), and *Vachellia tortilis* (Forssk.) Galasso & Banfi [syn. *Acacia tortilis* (Forssk.) Hayne], *S. ataxacantha*, *Senegalia caffra* (Thunb.) P.J.Hurter & Mabb. [syn. *A. caffra* (Thunb.) Willd.], *Senegalia nigrescens* (Oliv.) P.J.Hurter [syn. *A. nigrescens* (Oliv.)] and *Vachellia sieberiana* var. *woodii* (Burtt Davy) Kyal. & Boatwr. [syn. *A.*

sieberiana var. *woodii* (Burtt Davy) Keay & Brenan] (native species to South Africa). However, adults emerged only from *A. mearnsii*, *A. cyclops*, and *S. ataxacantha*, indicating that food availability may not be the only factor limiting the larval development (Rink 2013).

In view of its high seed infestation rates, *S. limbatus* has been suggested to play a role as biocontrol agent of invasive non-native *Acacia* species (Rink 2013). In South Africa, extensive biological control programs have been developed against invasive tree species, as, for example, the release of *A. macrophthalmus* for biological control of *L. leucocephala* in 1999 (Olckers 2004). Five seed-weevil *Melanterius* spp. (Coleoptera, Curculionidae) were introduced from Australia in different periods to reduce the invasiveness of *P. lophantha* and ten *Acacia* spp., including the three species investigated in the present paper, i.e., *A. mearnsii*, *A. saligna*, and *A. pycnantha* (Impson et al. 2011). Seed damage caused by weevils varied largely among sites and years from 4% to over 90%. Such variability was explained by a specific 4-year study on *Melanterius–Acacia* relationship and was mostly due to variable seed quality that resulted in low larval and pupal survival rates (Impson and Hoffmann 2019). Overall, seed-feeders are unlikely to effectively reduce the *Acacia* spp. density as a stand-alone control agent due to the extraordinarily high prolificacy of plants resulting in huge accumulation of long-lived seeds in the soil. In fact, effective results were obtained through the release of the flower-galling midge, *Dasineura rubiformis* Kolesik (Diptera, Cecidomyiidae) complemented by a seed-feeding weevil, *Melanterius maculatus* Lea (Coleoptera, Curculionidae), which caused a strong reduction of seed production of *A. mearnsii* (Impson et al. 2021). This reduction is expected to curb the accumulation rate of the seed banks and, in the medium-long term, reduce the spread of the invasive species. Besides a potential biocontrol agent of invasive plant species, further beneficial environmental effects by *S. limbatus* may be represented by the promotion of seed germination, e.g., on *Enterolobium contortisiliquum* (Vell.) Morong and *E. timbouva* Mart. (Meiado et al. 2013).

The present findings indicate the adaptability of *S. limbatus* to new host species when established in new areas. *Stator limbatus* also showed phenotypic plasticity in response to seed size or seed quality (Amarillo-Suárez and Fox 2006), in accordance with findings in other species (Hardy et al. 1992; Tsai et al. 2001). Moreover, this is consistent with results from studies showing that development time decreased and adult mass increased when insects developed on high quality hosts (Lindroth et al. 1991; Stockhoff 1993). Therefore, host shifts on local plants and new host associations cannot be ruled out in Europe in view of its ability to accept and adapt to local hosts. Adaptation to new or non-preferred host species has been observed on other coleopteran alien species, such as the red palm weevil *Rhynchophorus ferrugineus* (Olivier, 1790) (Coleoptera, Dryophthoridae) on the dwarf palm, *Chamaerops humilis* L. (Cocco et al. 2019). Importantly, *S. limbatus* has been reported on > 90 host species and ≥ 20 genera (de Jesús Parra-Gil et al. 2020), which is one of the widest host ranges within the Bruchinae. In view of its tropic spectrum, it has been classified as polyphagous, i.e., feeding in the seeds of various plant genera of different subfamilies (Ribeiro-Costa and

Almeida 2012; Yus-Ramos 2018). However, its host use is widely variable and it shows local specialization depending on the diversity of available host species (Morse and Farrell 2005a, 2005b). The establishment of *S. limbatus* in Europe and new associations with *A. pycnantha* and *A. saligna* required a redefinition and update of the bruchid host range to facilitate further research on its potential adaptation and spread in Europe. The exact definition of the host range of *S. limbatus* is not trivial due to nomenclatural issues within the family Fabaceae which have not been resolved (LPWG 2017). In addition, in a number of cases, the literature reported incorrect or partial names for the host plants. The bibliographic search analysis allowed to extend the global host range of *S. limbatus* to 111 species, in most part belonging to the mimosoid clade of the subfamily Caesalpinioideae (Fabaceae) (LPWG 2017). Synonym issues were resolved, e.g., *Acacia diversifolia* and *Leucaena diversifolia* both mentioned by Romero Gomez et al (2009) and synonymized in *Leucaena diversifolia* (Schltdl.) Benth, and up-to-date nomenclature provide the current and comprehensive overview of the feeding spectrum of *S. limbatus*. However, some old or unconfirmed reports would require further investigations, e.g., *G. max*, *Wallaceodendron celebicum* Koord., and *Arachis hypogaea* L. (Brian 1932; Kingsolver 2004). Since no previous records were found in literature, *A. pycnantha* and *A. saligna* are included in the present paper for the first time in the host range of *S. limbatus*.

This report of establishment of *S. limbatus* in Europe contributes to updating the insect worldwide distribution, which now includes North and Central America (native region), South America, South Africa, the Middle East, and southern Europe. Future research is required on known and potential host species in order to investigate its potential distribution and new host associations with native or non-native plant species (Parry et al. 2013). Studies on suitable climatic conditions for *S. limbatus* development will further assess the risks of spread in the Mediterranean Basin. Such surveys should include also urban habitats, in which seed feeders are frequently found (Branco et al. 2019).

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